SEASONAL CHANGES IN BODY WEIGHT AND FAT AND THE RELATION OF FATTY ACID COMPOSITION TO DIET IN THE WILLOW PTARMIGAN[1]

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Willow Ptarmigan (*Lagopus lagopus*) live throughout the year in the arctic and subarctic of North America and Eurasia. Their presence in large numbers indicates that they are well adapted to their environment which may at times be extremely cold and stormy. Populations of these birds nest in the Alaskan far north and portions of the population migrate south through passes in the Brooks Range to winter in the sheltered valleys which contain large stands of willow and south of the tree line, spruce (Irving et al., 1967*a*). The diet of Willow Ptarmigan consists of over 97 per cent willow buds and twigs during the winter months in the arctic, and of 89 per cent willow in the subarctic, while during the summer the birds shift to green vegetation, usually leaves and berries (West and Meng, 1966; Weeden, in press).

Through a series of investigations, we are trying to understand how the ptarmigan are adapted to their life in the arctic. We have seen that the population segregates into sex and age groups during the course of its migration and on their wintering grounds so that the four categories pursue different winter programs (Irving et al., 1967*a*). Ptarmigan expend approximately the same amount of energy at all seasons and their special seasonal energy demanding activities are distributed throughout the year to maintain a steady level (West, in press). Studies on the feeding habits of the ptarmigan show that they accumulate large quantities of willow in their crops during short winter days while during summer their crops remain uniformly light throughout the long days (Irving et al., 1967*b*).

While processing the birds for their crop contents, we noticed that there was considerable difference in net body weight (whole weight less crop weight) of birds among the four recognizable age-sex categories: adult male, adult female, juvenile male, and juvenile female. It was therefore essential to examine samples of each component of the population to determine if there were seasonal changes in weight and fat. In addition to fats in essential structures, fat in variable reserves represents accumulated provision for energy at rates exceeding dietary intake. Fat accumulation depends upon many environmental factors as well as on the food of the bird and the metabolic state of the bird at the time of fat deposition. We have recently gathered evidence that the fatty acid composition of many of the willows

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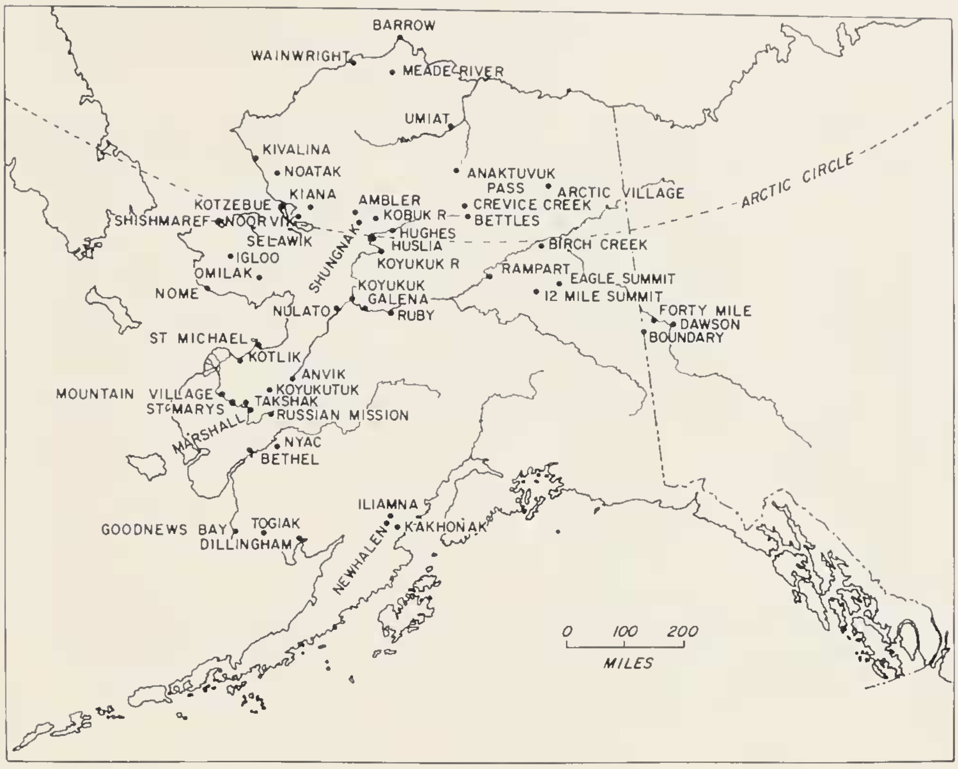

Fig. 1. Map of Alaska and adjacent Yukon Territory showing collecting locations of Willow Ptarmigan.

eaten by the Willow Ptarmigan changes significantly from one season to another (West and Meng, unpublished). We also wanted to see if fatty acids of the diet were incorporated unchanged into the fatty acids in the depot fat of the ptarmigan. This would provide a prime example of a specialist bird incorporating certain fats, in this case willow fats, into its own composition. If ptarmigan proved to be a "willow bird" by virtue of its fat we might then anticipate finding other species of birds with their fat marked by reason of their diet. In this way, we might in the future be able to trace a migratory pathway or at least to tell from where a bird has come by allocating its fatty acid spectrum to the various dietary sources.

METHODS

Willow Ptarmigan were collected by shotgun throughout the year in the Brooks Range of northern Alaska (Fig. 1) specifically at Umiat (69° 24′N., 152° 07′W.), Anaktuvuk (68° 10′N., 151° 46′W.), Crevice Creek (67° 22′N., 152° 04′W.), and Bettles Field (66° 55′N., 151° 28′W.). Individuals collected from these areas are part of a morphologically homogeneous population as determined from wing and tail measurements of over 1200 samples (West et al., 1968). All data on fat and fatty acid composition of ptarmigan were taken from these collections. Additional birds (1400), collected by resident people in villages throughout Alaska, are also included in the net weight analysis. By employing a Duncan's multiple range test it was possible to show that the weights of the ptarmigan collected from the other areas in each of the four age-sex groups were not statistically

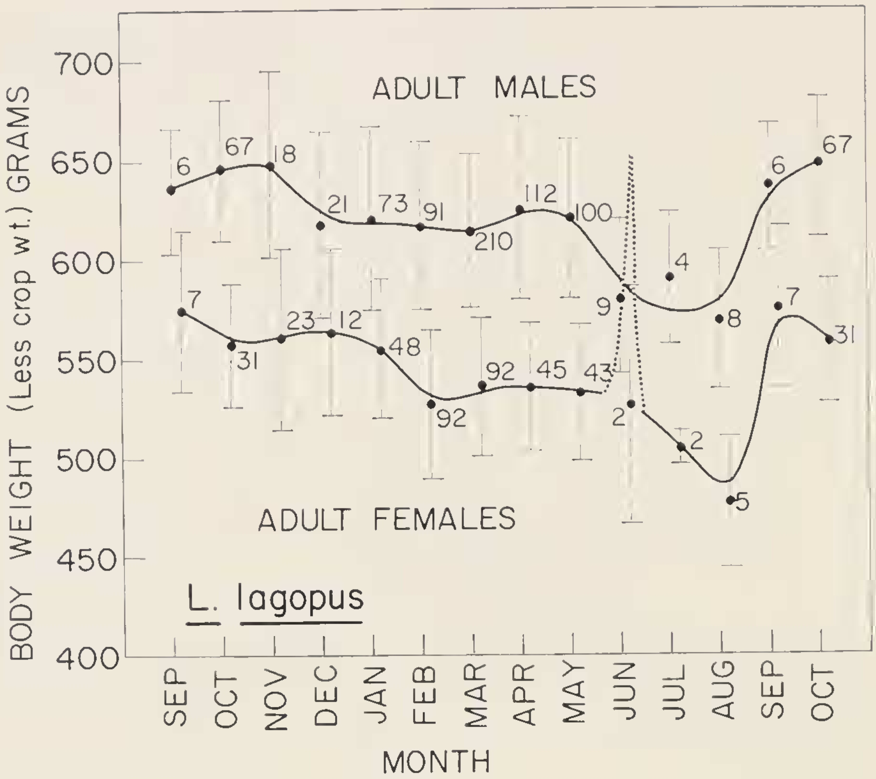

Fig. 2. Seasonal changes in body weight (less crop weight) of adult Willow Ptarmigan. Number beside mean represents sample size; vertical lines indicate one standard deviation. The dotted line for adult females in June indicates the assumed increase in weight due to egg formation (not recorded in the two females shown here collected after egg laying).

different from those collected in the Brooks Range (West et al., MS). The areas of collection are shown in Figure 1.

Birds were frozen in plastic bags immediately after shooting and shipped to the Institute of Arctic Biology for processing. Here they were thawed, weighed, the crop removed and weighed, the bird aged and sexed, and the wing and tail measured. Since weights of crops varied from about 3 grams when empty to 100 to 120 grams when full, the weight of the whole bird minus the crop weight (= net weight) was used in all analyses.

Seventy-nine samples of subcutaneous depot fat taken from the interclavicular area of birds selected at random from collections were analyzed for their fatty acid composition. In addition 82 birds were selected at random from fall, winter, and spring samples for total lipid content and fatty acid composition. The digestive tract, feathers, feet, and manus of the wings were removed prior to grinding and drying. Birds were ground in a large meat grinder and then either dried in air at 80 C or frozen and lypholized. An aliquot of the resultant dry material was extracted using petroleum ether (30–60 C boiling point) in a Soxhlet extractor. Following extraction the lipids were saponified using alcoholic KOH. The depot fat samples were saponified directly. The non-saponified fraction was discarded and the fatty acid salts were converted to free fatty acids with HCl. The fatty acids were converted to their methyl esters by boron trifluoride methanol and chromatographed on DEGS (diethylene glycol succinate) in an F and M hydrogen flame chromatograph. Peaks were identified using standard fatty

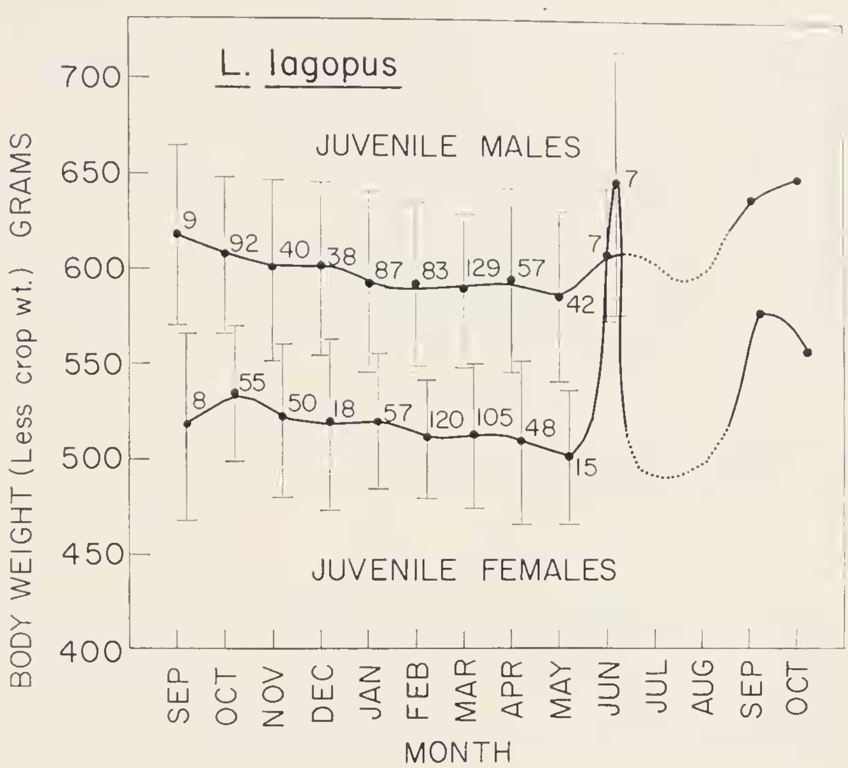

FIG. 3. Seasonal changes in body weight (less crop weight) of juvenile Willow Ptarmigan. Number beside mean represents sample size; vertical lines indicate one standard deviation. Dotted line indicates assumed summer weights. Juveniles in their second September and October are classed as adults. Therefore, the points for these two months are taken from Fig. 2.

acids and by using Ackman's (1963) technique of plotting the logarithm of the relative retention time to stearic acid (C_{18}) against carbon numbers. Peaks were triangulated and areas used to calculate the relative per cent of each acid.

RESULTS

Body Weight.—Adult males were heavier than adult females at all seasons (Fig. 2). Weights were highest during the fall (October and November), declined slightly during the winter and showed a slight peak during April and May. Males showed a decline in body weight in early June while they were undergoing courtship and territorial activities. They reached their lowest weight in August and then climbed rapidly to the maximal weight in October and November. Adult females likewise had a high peak in September, a low in February and a slight rise in April. Their decline began later in the summer than that of the males. The summer low came after egg laying and during the time of care of chicks and reached its lowest point in August. There was an increase of about 100 grams between August and September when the females reached their maximum weight.

First year birds (determined by the presence of the bursa of Fabricius prior to January or by the presence of a darkly pigmented ninth primary

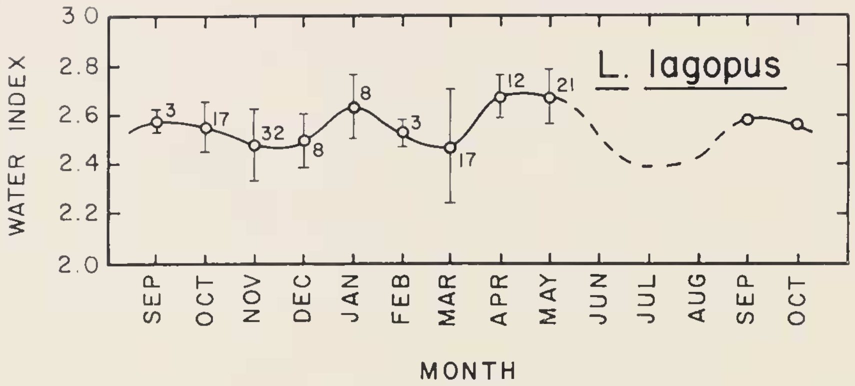

FIG. 4. Seasonal variation in water index (grams water/fat-free dry weight) of Willow Ptarmigan carcasses from the Brooks Range.

feather (West et al., 1968) did not show the same abrupt changes in body weight as did the adults (Fig. 3). Juvenile males however were heavier than the juvenile females at all seasons except briefly during egg laying when weights of collected females were higher than those of males at any season. Weights were highest for juvenile males in September and declined gradually until May. We have no records for the middle of the summer. Juvenile females had their highest weights in October and declined during summer. Females, which breed in their first year, while forming and laying eggs had

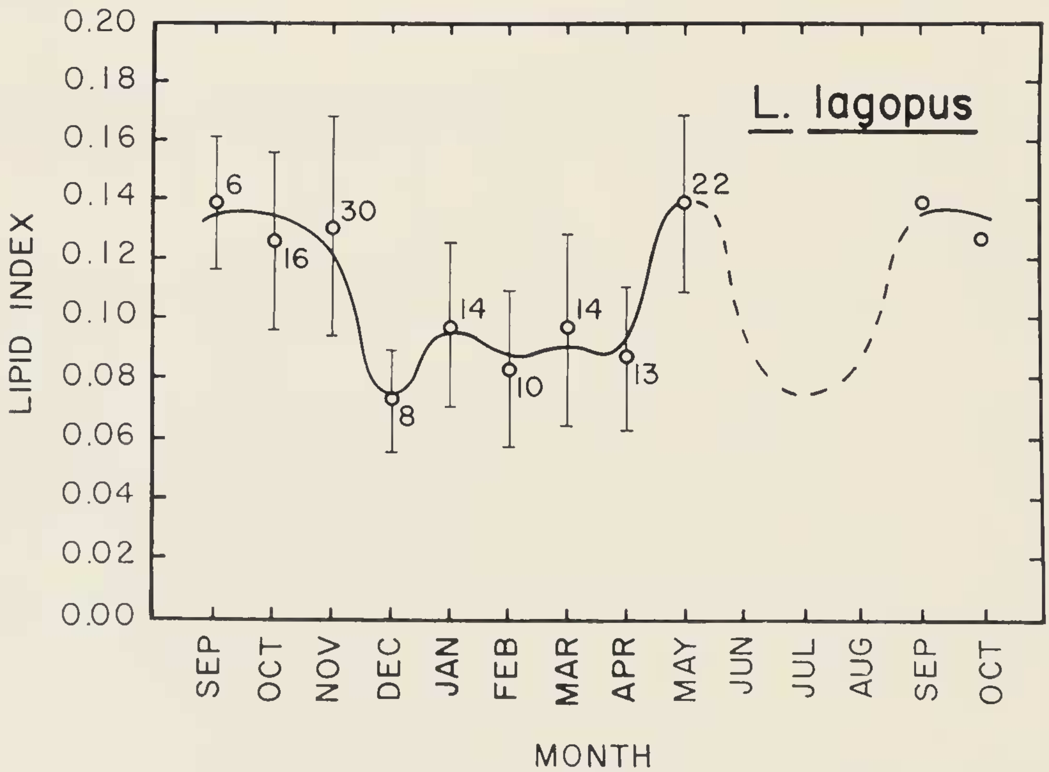

FIG. 5. Seasonal variation in fat index (total ether extractable lipid, grams/fat-free dry weight) of Willow Ptarmigan carcasses from the Brooks Range.

TABLE 1

	Fat-free dry weight (g)		Wing length (mm)*	
	n	Mean ± SD	n	Mean ± SD
Adult Male	20	108.56 ± 10.34	416	205.6 ± 4.7
Adult Female	16	95.24 ± 10.25	165	192.0 ± 4.1
Juvenile Male	19	96.35 ± 8.45	329	201.8 ± 5.2
Juvenile Female	23	87.73 ± 10.35	225	190.1 ± 5.1

* West et al., 1968.

weights almost 150 grams higher than those collected in May before egg formation had taken place.

Body Water and Fat.—There was no statistically significant difference in the proportion of water in the carcasses of different age and sex categories ($p > 0.10$). Body water, calculated as the water index (weight of water/fat-free dry weight of carcass) fluctuated throughout the year being significantly higher in January and April–May than in November and March respectively ($p < 0.01$) (Fig. 4).

Body fat was determined as the lipid index (weight of fat/fat-free dry weight). The fat-free dry weights of carcasses varied significantly among the four age-sex categories (Table 1) but did not vary with time of year from September through May. No values were obtained on summer birds. Lipid indices were therefore calculated for each bird based on the weight of ether-extracted lipid and the mean fat-free dry weight for its age-sex category.

There were no statistically significant differences in lipid index between ages or sexes in any month ($p > 0.4$), but there were statistically significant differences between months of the year (Fig. 5). The index for December was significantly lower than that for either November ($p < 0.01$) or January ($p < 0.05$) and there was a significant rise from April to May ($p < 0.001$).

Fatty Acid Analysis.—The predominant fatty acids in either the total lipids or depot lipids of Willow Ptarmigan are 16- and 18-carbon acids as shown in the two sample chromatograms (Fig. 6). The most abundant acid in the total lipids is linoleic acid ($C_{18=2}$) (Fig. 7). There are significant amounts of 22-carbon acids. There are a few small seasonal changes in fatty acids that can be noticed in Fig. 7; the amount of stearic acid (C_{18}) and docosenoic acid ($C_{22=1}$) increased significantly from fall to winter. At the same time there was a sharp decrease of oleic ($C_{18=1}$) and linolenic acid ($C_{18=3}$). There appeared to be no significant changes between winter and spring. Unfortunately we did not retain specimens for fat analysis for the summer months.

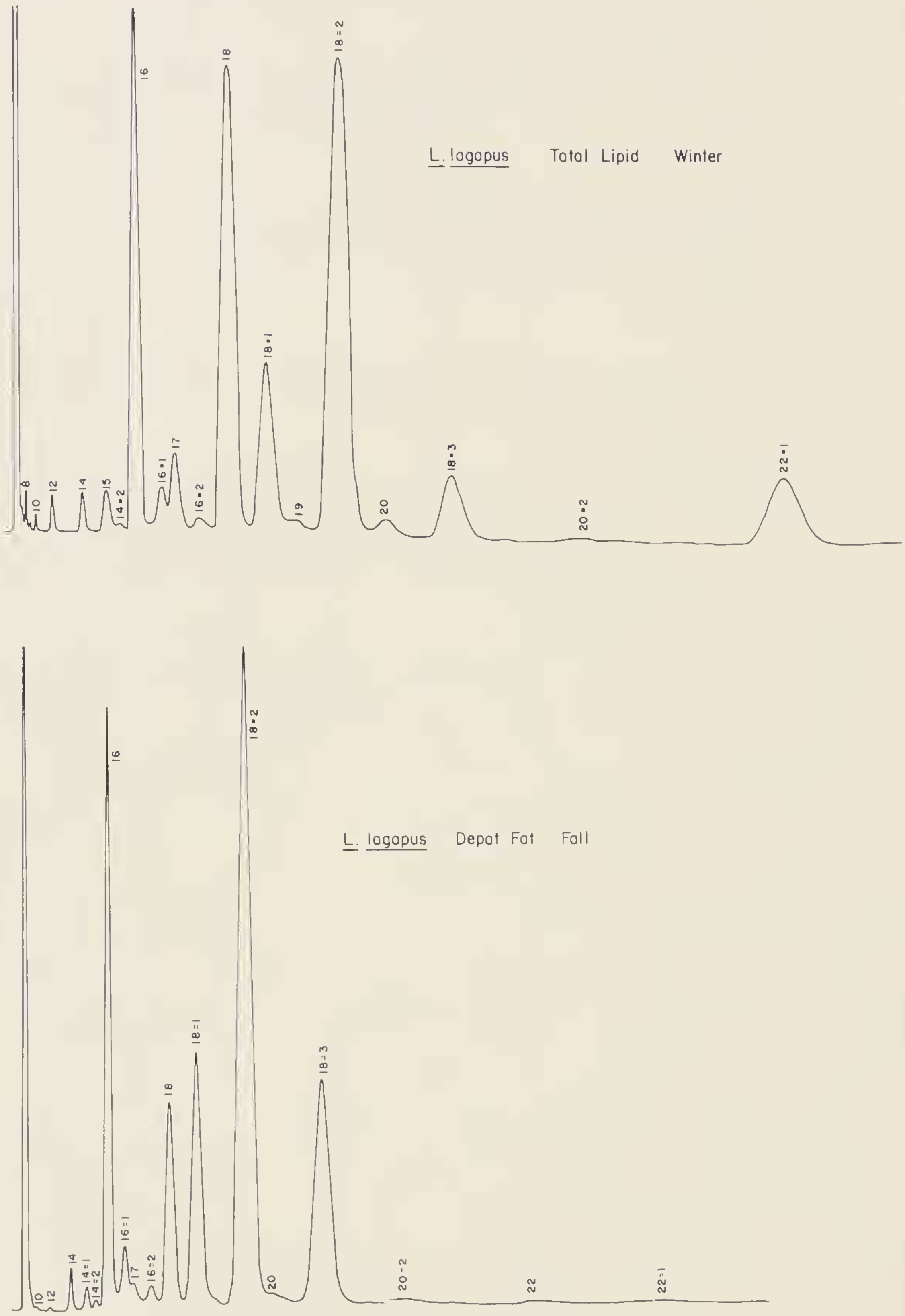

Fig. 6. Sample gas chromatograms of total lipid and depot fat fatty acids of Willow Ptarmigan from the Brooks Range. Each peak represents one fatty acid; the area under the peak indicates relative proportion of acids. Numbers represent length of the fatty acid carbon chain with the number of unsaturated bonds following the =.

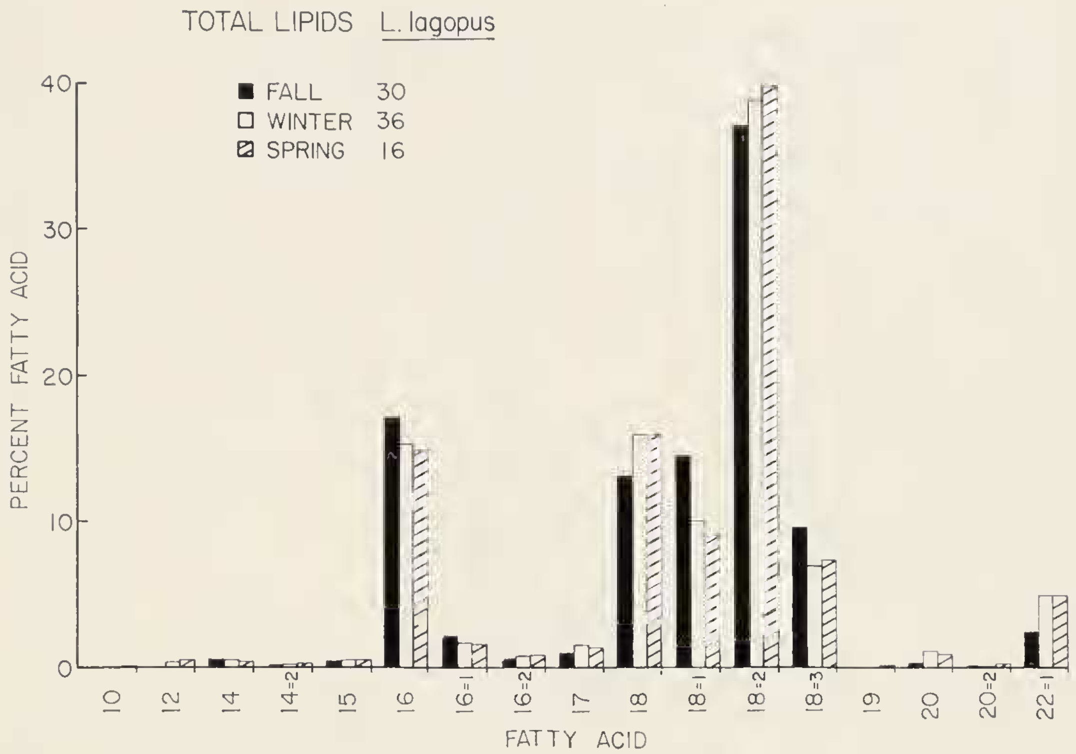

FIG. 7. Seasonal shift in proportion of fatty acids in the total ether extractable lipids of Willow Ptarmigan from the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

Depot fat fatty acids presented a picture somewhat similar to that found for total lipid fatty acids with the 16- and 18-carbon fatty acids being predominant (Fig. 8). One exception was that the longer chained fatty acids were not as abundant. The same seasonal shifts occurred in depot lipids as occurred in the total lipids with a decrease in palmitic acid (C_{16}) oleic, and linolenic acid from fall to winter and a concomittant increase in stearic, linoleic, and arachidic (C_{20}) acids. Birds in winter had a higher content of linoleic acid than at any other season. The amount of linoleic acid decreased in spring while the amount of palmitic, oleic, and linolenic acid increased in the spring.

DISCUSSION

Body Weight, Fat, and Water Content.—The marked seasonal changes in net body weight of adult Willow Ptarmigan correspond with observed seasonal changes in activity and energy requirements of the birds and parallel the weights of captive birds (West, in press). The high weight of adults in November and April–May correlate with times of high water and lipid content. The peak in high water and lipid indices in January does not match an increase in weight and is unexplained at present. The spring and fall increases in fat correlate with time of migration of Willow Ptarmigan

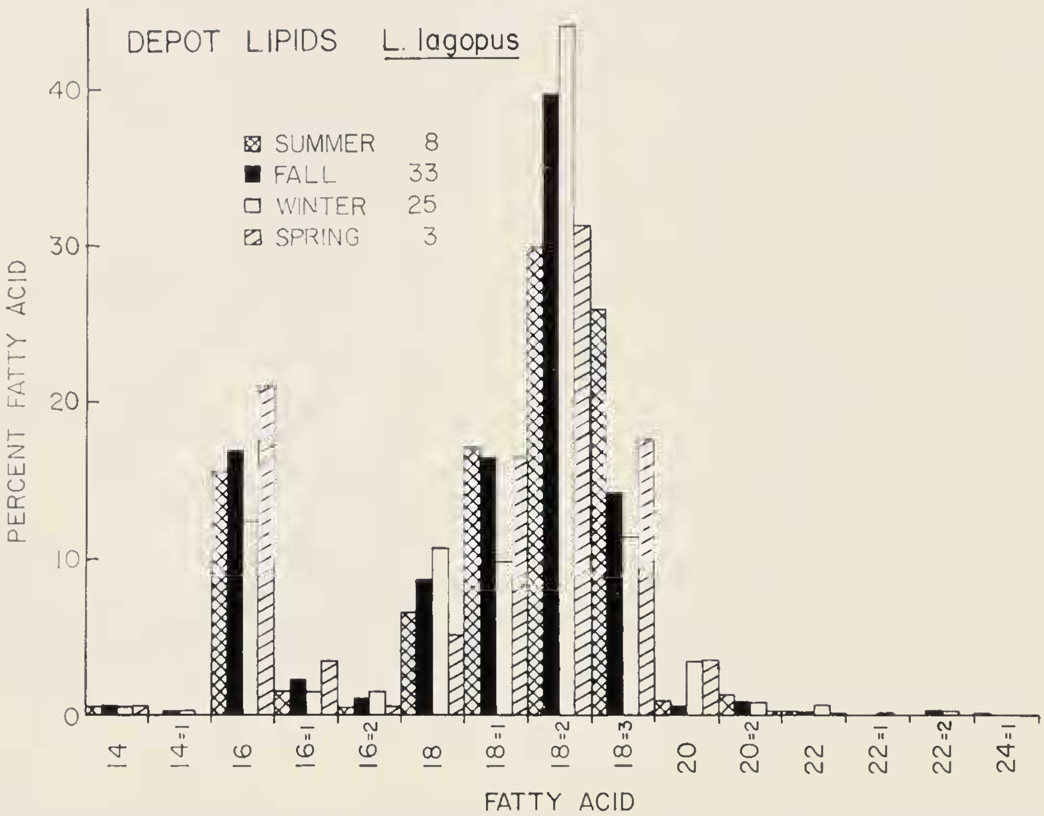

Fig. 8. Seasonal shift in the depot lipids of Willow Ptarmigan from the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

in the Brooks Range (Irving et al., 1967*a*). The amount of fat deposited however was slight in comparison with that required for long distance migrants (Odum, 1965; Odum and Connell, 1956). There was a slight depression in weight during the middle of the winter when cold and wind occasionally impede feeding and may have their greatest metabolic effect but in general the fall, winter, and spring body weight level is greatly elevated above that of the summer. First males and then females decreased in body weight during the early summer and increased with great rapidity between August and September. Males decreased in weight between May and June during the time of territory defense and courtship. Females decreased in weight between June and July in the time following egg-laying and during incubation and continued their decline into August perhaps due to the energy demanding stresses of parental care. Molt, which begins in May in males and June in females, continues all summer until early October, except during egg laying (West, in press) and incubation (Weeden, pers. comm.), and places a continuing energy burden for feather synthesis and possibly for thermoregulation on all birds. Although it is not shown in Figure 2, adult females undoubtedly become extremely heavy briefly in

June during egg formation and laying. Our June sample was not taken at the right time to show this for adults but, as with the juvenile females shown in Figure 3, there must have been a sudden (30 per cent) increase in feeding and an increase in body weight contributing to formation of eggs prior to egg laying. This sudden increase in weight has been documented by Irving (1960) for passerines and sandpipers just prior to egg laying, and noted also by Weeden (pers. comm.) for Rock Ptarmigan (*Lagopus mutus*).

Juvenile females become fully grown or equivalent in size to the adult female in their first spring and undergo a complete breeding cycle during their first year as evidenced by the presence of fully formed eggs in the oviducts. Although both juvenile males and juvenile females make migrations comparable to that of adult females they did not show the two pronounced peaks in weight of the adults during spring and fall. Juveniles are evidently still growing in their first winter and the addition of protein results in less weight decline in winter than the adults.

The general pattern of body weight change in Willow Ptarmigan was similar to that of the non-migratory Ruffed Grouse (*Bonasa umbellus*) in that there was a slight decline during late winter, a sharp rise during the spring, and a fall in the summer in birds collected in New York (Bump et al., 1947). However, the Ruffed Grouse did not show a distinct peak in fall. Juvenile Ruffed Grouse showed the same weight pattern as the adults after May and showed a rather steady increase in weight in their first fall, reaching adult weight in spring. In Willow Ptarmigan there is an abrupt increase in weight that occurs only in the bird's second (and subsequent) autumn and there is no evidence of an increase during the first winter.

Koskimies (1958) has shown that total body weight (with crop) of the Finnish Capercaillie (*Tetrao urogallus*) and Blackgame (*Lyrurus tetrix*) increased slightly from September through November then declined in December. Increases were greater for juveniles than for adults. The situation with Willow Ptarmigan varies with age and sex and only adult males achieved a weight maximum in November. The small sample sizes in September in all four categories of Willow Ptarmigan make comparisons difficult, but it appears that adult males lost weight in winter before adult females, perhaps because they remain farther north in a climate that gets colder earlier and where energy requirements may be higher (Irving et al., 1967*a*; West, in press). Adult females which migrate south along with the juvenile females did not lose weight until February when their weights did not abruptly change but continued to fall gradually throughout the winter.

Siivonen (1957) stated that the weight cycle of adult tetraonid females differs from that of males in that the former has two weight peaks per year and the latter only one. Alaskan Willow Ptarmigan appear to be an exception to this rule since both sexes show two weight maxima: males in October–November and April–May; females in September–December and again in early June.

Odum and his associates have assumed that the fat-free dry weight of a single species remains constant throughout the year for birds of similar wing length (Odum and Connell, 1956; Connell, Odum, and Kale, 1960). The fat-free dry weight of Willow Ptarmigan carcasses differs significantly with age and sex, and these categories also differ significantly in wing length (Table 1). Although we could not demonstrate statistically significant seasonal differences in fat-free dry weight, the data show peaks in fall and spring with a low in winter. Samples are lacking for summer but observation by us and by Robert Weeden indicate that summer birds, especially incubating and brooding females, lose a significant amount of body mass in summer. These observations need documentation. We cannot now see why there are significant seasonal changes in water indices of Willow Ptarmigan. The seasonal shifts do not follow the changes in fat precisely (Figs. 4, 5). In fall, the water index falls prior to fat; in spring, the water index rises prior to fat, and in mid-winter, they both rise together. Some animals show increases in water volume which are either due to acclimation to cold or heat (Hart, 1964) but we are not aware of any studies of water content throughout the year in wild birds.

The seasonal change in lipid index may be related to a number of factors such as preparation for migration in fall and spring or preparation for summer breeding and for winter cold stress. However, the changes in fat index which vary from 0.07 in December to 0.14 in September and May, represent a difference of only 6.5 grams of fat. This would amount to a little over 60 kilocalories, or less than one-third of the average daily energy requirement of wild Willow Ptarmigan (West, in press). Obviously ptarmigan are not fat birds at any time of the year unlike many passerines, and the fat deposited in the body does not constitute a substantial energy reserve.

Fatty Acids.—The composition of fatty acids in the diet of Willow Ptarmigan has been compiled from data obtained on all of the plant species which are present in the ptarmigan diet (West and Meng, 1966) (Fig. 9). Fatty acid composition was determined by gas chromatography for each species independently (West and Meng, unpublished) and Figure 9 represents a proportional configuration of the fatty acid composition of the diet. The diet consists largely of 16-, 18-, 20-, 22-, and 24-carbon acids. The predominant acid is linoleic acid (C_{18-2}).

There are marked changes in the diet lipid composition with season. From summer to fall there was an abrupt decrease in palmitic (C_{16}) and linolenic (C_{18-3}) acid and an increase in linoleic (C_{18-2}), arachidic (C_{20}), behenic

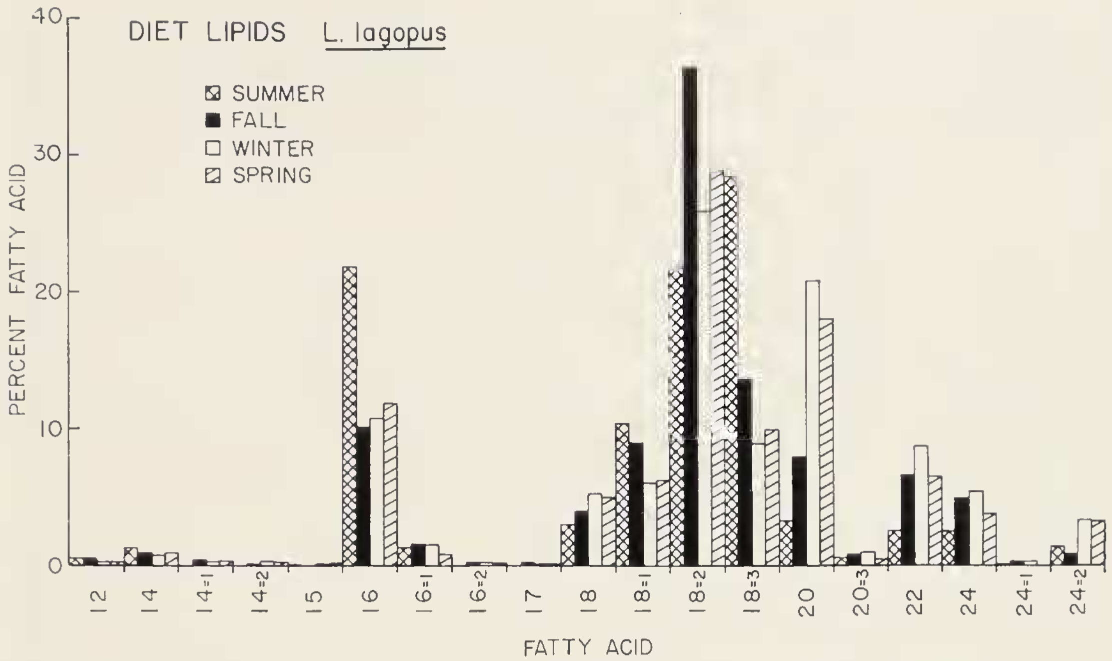

FIG. 9. Seasonal changes in the fatty acids consumed in the diet of Willow Ptarmigan in the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

(C_{22}) and lignoceric acid (C_{24}). The abrupt changes in these acids reflect the shift in the ptarmigan diet from the summer one of leaves and berries which are high in palmitic (C_{16}) and linolenic ($C_{18=3}$) acids to the fall one of willow buds and twigs. From fall to winter there were increases in stearic (C_{18}), arachidic (C_{20}), behenic (C_{22}) and tetracosadienoic ($C_{24=2}$) acids. and decreases in oleic ($C_{18=1}$), linoleic ($C_{18=2}$) and linolenic ($C_{18=3}$) acids. The increases in the saturated and long-chain fatty acids are due to the changes that occur in willows from fall to winter (West and Meng, unpublished). The increases in saturation, especially in the arachidic acid (C_{20}) fraction, coincides with an increase in saturated triglycerides in the sheathes of the willow buds. There were small differences in fatty acid composition from winter to spring when the diet shifted slightly to include exposed *Dryas* leaves and other low vegetation (West and Meng, 1966). It will be noticed that the spectrum of fatty acids in the diet ranges from 12–23 carbon chains with the majority located in the 16- and 18-carbon number groups.

When the diet lipids are compared with the total lipids or especially with the depot fat situation (Figs. 7, 8. and 9), it is obvious that the ptarmigan are "willow birds" in that their fatty acid composition resembles that of the major fatty acids in the diet closely even to the point of including in total lipids appreciable amounts of 20 to 22 carbon acids, unusual in vertebrate fats. Linoleic acid ($C_{18=2}$) is the predominant acid in both diet and bird. The abrupt seasonal changes in fatty acid composition of the diet lipids was not present in the total lipid fraction. The changes from fall to winter in increased saturation and chain length are not evident in either the total lipids nor in the depot lipids. One striking feature was the reduction in amounts of acids with a chain length greater than 20 carbons that occurred when diet fatty acids are converted into depot fat fatty acids by the bird. The alterations that occur from diet lipid to depot lipid can occur either through bacterial action in the cecum or through transformation in the liver. It is also possible that there is a differential retention and deposition of certain acids. Therefore, although the general picture of ptarmigan depot lipids is similar to that of their diet, the great changes that occur in diet lipids between seasons is not clearly reflected in the depot fats.

Although a great deal of work has been done on the effects of diet lipids on the lipid composition of laboratory animals (Edwards et al., 1962; Beare and Kates, 1964; Carroll, 1965; Feigenbaum and Fisher, 1959; Machlin et al., 1962) and humans (Imaichi et al., 1965) very little has been done on wild birds with the exception of our recent work on Common Redpolls (*Acanthis flammea*) (West and Meng, 1968) and that of Moss and Lough (1968) on four species of game birds. With redpolls it was possible to show that there were great changes in depot fat composition between spring migrating birds and those during the breeding season and that these differences may have been due to different seed diets in the wild. However, redpolls in captivity did not alter their depot fat fatty acid composition when fed experimental diets that had different fatty acid compositions.

Moss and Lough (1968) investigated the depot fat fatty acid composition of two Red Grouse (*Lagopus lagopus scoticus*) a close relative of the Willow Ptarmigan (*Lagopus lagopus alascensis*) under discussion here. The Red Grouse is sedentary and its diet consists mainly of heather (*Calluna vulgaris*) unlike the migratory and willow-eating Willow Ptarmigan. The major depot fat fatty acids of both birds closely resemble that of their respective diets. Both diets are high in linoleic acid ($C_{18=2}$) as are the depot fats.

Walker (1964) in studying the major fatty acids in some migratory birds, showed that there were definite species differences which could have been related to diet. In all of the species she studied however, oleic acid ($C_{18=1}$) was the predominant component. Even the herbivorous Bobolink (*Dolichonyx oryzivorus*) had conspicuously less linoleic ($C_{18=2}$) than oleic acid ($C_{18=1}$). In the Willow Ptarmigan and Common Redpoll, both herbivores, the predominant acid was linoleic ($C_{18=2}$).

In making the generalization that depot lipids of birds are largely derived from the diet, caution should be exercised since the work with redpolls indicates that with increased fat deposition from different diets a more uniform fatty acid composition of the depot fats results. We still do not know the complete role of the cecal microbiota in synthesizing fatty acids (McBee and West, 1968) and at the present we cannot be certain if all of the essential fatty acids are directly derived from diet or are synthesized in the cecum.

SUMMARY

Body weight less crop weight of adult Willow Ptarmigan from western, northern, and central Alaska are higher in fall and in spring than in winter in periods corresponding to migration of these birds. Summer weights are much lower than winter weights. The decline in weight corresponded to the time of courtship and territory defense in males, and to post-egg-laying incubation and parental care in females. During egg formation and laying, weights of juvenile females and presumably adults, were higher than at any time of year. Juvenile ptarmigan reach a maximum juvenile weight in their first fall and then gradually decline in weight throughout their first winter and spring. Juveniles can no longer be distinguished from adults by known morphology after their second fall and their weights are then included in the adult weights and at that time show a marked increase over summer.

Water index of Willow Ptarmigan carcasses (whole bird less digestive tract, feathers, feet, and wings from the wrist distally) varied from September through May being significantly higher in September, January, and April–May than in those months preceding. Lipid index (ether extractable lipids) of Willow Ptarmigan carcasses varied with the change in body weight being high in fall and spring and lower in winter. However there was a significant increase in January not related to body weight. Although no data are available for summer birds, it is assumed that fat decreases with body weight.

There is a direct correlation of diet fatty acids with those deposited in the bird either as total lipids or as interclavicular depot lipids. The predominant acids are 16- and 18-carbon chains with the most abundant being linoleic acid ($C_{18=2}$). The long chain fatty acids (C_{22}–C_{21}) present in the diet are poorly represented in the total lipids and in only trace amounts in the depot lipids. The marked seasonal shifts in diet fatty acids are not pronounced in the birds' fat. This indicates that although the general pattern of diet and bird fatty acids are similar, small seasonal changes are not evident and certain long chain fatty acids in the diet are either not utilized or converted to other forms by the bird.

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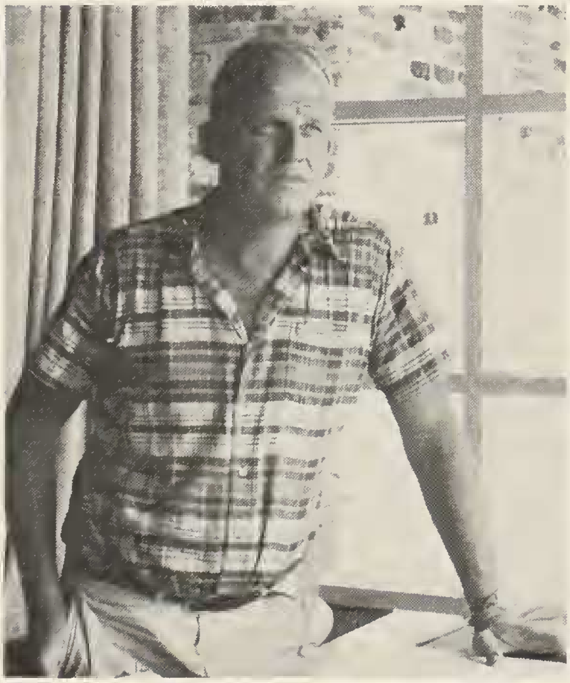
NEW LIFE MEMBER



Mr. John H. Dick of Meggett, South Carolina has recently become a Life Member of The Wilson Ornithological Society. Mr. Dick is well known to most members of the Society as the outstanding bird artist whose paintings and drawings were featured in such books as "Warblers of America," "A Gathering of Shorebirds" and "The Bird Watcher's America." Besides his painting Mr. Dick is engaged in an active program of field work and bird photography. He also maintains a collection of live waterfowl, which was visited by some members of the Society on the occasion of the Charleston meeting in 1963. Mr. Dick attended Brooks Prep School and the Yale Art School, and is a member of the AOU and the Cooper Society.